Biol Theory (2013) 7:38–47
DOI 10.1007/s13752-012-0070-2

LONG ARTICLE

Selection, Drift, and Independent Contrasts: Defending the Methodological Foundations of the FIC

Armin W. Schulz

Received: 15 May 2011 / Accepted: 18 October 2012 / Published online: 13 November 2012

Abstract Felsenstein's method of independent contrasts (FIC) is one of the most widely used approaches to the study of correlated evolution. However, it is also quite controversial: numerous researchers have called various aspects of the method into question. Among these objections, there is one that, for two reasons, stands out from the rest: first, it is rather philosophical in nature; and second, it has received very little attention in the literature thus far. This objection concerns Sober's charge that the FIC is methodologically flawed due to its (seemingly) resting on the assumption that the traits it studies evolved by drift—and thus ruling out selective hypotheses from the start. In this article, I try to rebut this charge. To do this, I first consider a preliminary conceptual worry—the question of how it is even possible for two drift-driven traits to be evolutionarily correlated—and show that it can be answered by noting that the FIC can be seen as being concerned with the investigation of the modularity of the relevant traits. Given this, I then show that Sober's methodological charge can at least be mitigated by noting that the assumptions behind the FIC do not in fact preclude it from investigating selective hypotheses. I end by pointing out that making this clearer is not just relevant for defending the cogency of the FIC, but also for developing a deeper understanding of correlated evolution in general.

Keywords Brownian motion · Idealization · Internal selection · Modularity

One of the most prominent comparative methods—appealed to in many contexts from botany to zoology and human evolution—is Felsenstein's method of independent contrasts, or FIC (see Felsenstein 1985, 2004, Chap. 25; Harvey and Pagel 1991, Chap. 5).[1] Despite this prominence, though, this method is also very controversial. In particular, various researchers have questioned its general plausibility and practicality, leading to vigorous responses by defenders of the method and equally vigorous counter-responses by the attackers (e.g., Harvey et al. 1995a, b; Westoby et al. 1995a, b; Freckleton et al. 2002; Felsenstein 2002, 2004). As I try to make clearer in this article, though, there is one—rather philosophical—worry surrounding the method that, while sometimes pointed out, has not yet received the attention it deserves: namely, that the FIC is *conceptually or methodologically flawed*.

In particular, it is sometimes claimed that the FIC presumes that the traits it studies have evolved by drift—even though determining the selective history of these traits is precisely what the method is meant to be used for (for a particularly explicit version of this charge, see Sober 2008, pp. 252–253).[2] Addressing this worry is the aim of this article. As it turns out, doing this is not just interesting for a defense of the cogency of the FIC, but also because it

A. W. Schulz (✉)
Department of Philosophy, Logic, and Scientific Method, London School of Economics and Political Science, London, UK
e-mail: a.w.schulz@lse.ac.uk

[1] Recently, a different type of method, Phylogenetic Generalized Least Squares (e.g., Bulmer 1991), has become popular as well; however, it remains true that the FIC occupies a central position in this area.

[2] A somewhat related worry could also be raised for many methods of phylogenetic inference. For example, maximum likelihood methods typically assume that the relevant characters evolved by drift (e.g., Harvey and Pagel 1991; Felsenstein 2004), even though the results of this analysis are often used to test the claim that these characters have evolved by natural selection (e.g., through doing comparative studies). However, to make the discussion more tractable, I will restrict myself to discussing only the FIC here.

brings out several issues of interest for our understanding of biological evolution in general.

The article is structured as follows. In the next section, I briefly present the aims and outlines of the FIC approach. I then spell out Sober's charge that the method is methodologically flawed, and lay out a related preliminary conceptual worry. In the following two sections, I respond to the conceptual worry and Sober's methodological objection. Finally, I briefly consider some general insights that come out of the discussion, and then conclude.

Felsenstein's Method of Independent Contrasts

In order to most easily present the methodological worries concerning the FIC, it is best to begin by briefly laying out the background, abstract structure, and aims of the method. To do this, start by assuming that we want to find out about the evolution of two continuous traits, *X* and *Y*, across a set of taxa. For example, assume that we have the suspicion that these two traits have evolved by natural selection, and that we want to investigate this suspicion in more detail. More generally, assume that we are looking for evidence concerning what the evolution of these two traits was like—*which* factors determined this evolution, and *how* did these factors determine it?

Now, importantly, finding out about a *correlation* in the evolution of these two traits would seem to be tremendously useful in this regard. Most directly and obviously, such a correlation could be taken as evidence for the fact that the two traits are *adaptations*: after all, it seems that a simple and direct explanation for why the two traits are evolutionarily correlated is that natural selection is driving both in a similar manner.[3] The FIC provides a means for testing for the existence of this kind of correlation.

Note that in order to establish this existence, the key problem that has to be solved is the fact that the trait values in different taxa are not independent data points (due to the fact that the different taxa all have a common ancestor; Felsenstein 1985). The FIC tries to solve this problem by noting that whatever may be true about the absolute values of the traits, the *differences* between them must be statistically independent. That is, leaving aside the starting values of the two traits deeper in the phylogeny, if there is a correlation in the evolution of the two traits, it must at least be true that *changes* in *X* go with *changes* in *Y* (whatever their actual values are). Made more precise, this insight is sufficient to solve the problem of establishing correlation among the values of the traits without falling prey to distorting phylogenetic influences.

In more detail, the FIC approach can be set out in the following three-step procedure (see also Felsenstein 1985, p. 10):

1. Compute the values of the interior nodes by adjusting the arithmetic average between the descendent nodes for any differences in the respective branch lengths (i.e., in the lengths of time and rates at which different taxa have been evolving).[4]
2. Compute the contrasts of the two traits among the tip species, and among the estimated interior nodes.
3. Test for a correlation among the contrasts.

However, it also needs to be noted that this method rests on several key assumptions whose truth is necessary in order to get it off the ground (see also Felsenstein 1985). Among the most important of these assumptions are the following three (see also Diaz-Uriarte and Garland 1996, pp. 27–28):

(i) The phylogeny is known.
(ii) The branch lengths are known.
(iii) The evolution of the traits in question follows Brownian motion (i.e., a random walk).

Assumption (i) is necessary as without knowledge of the phylogeny, no independent contrasts could be computed: it would then not be clear what these contrasts *are*. Assumption (ii) is needed as ignoring differences in the various branch lengths would introduce biases into the values of the interior nodes. Assumption (iii) is needed as for us to be able to even begin to compute the values of the interior nodes, we need to have some idea about how the trait values change over time—otherwise, it will not be possible to infer their ancestral states. The assumption of Brownian motion helps in this as it entails that for any given starting value of trait *X*, it is just as likely that X *increases* in value as that it *decreases* in value (and similarly for *Y*); for this reason, the best estimate of the values of *X* and *Y* of the ancestral nodes is the arithmetic average of the values of *X* and *Y* of the descendent taxa. For what follows below, it is this assumption in particular that is important to keep in mind.[5]

[3] As we will see momentarily, though, there might also be other reasons for the existence of the correlation.

[4] Note that the reason why we need to calculate the values of the interior nodes is that what we are interested in (at least in most cases) is establishing a correlation in the evolution of traits *X* and *Y in general*—not just in that of *X* and *Y in the tip taxa* (see also Westoby et al. 1995a, b; Felsenstein 1985, pp. 5–6). For details of the calculations—which are not so important here—see, e.g., Felsenstein (1985) and Harvey and Pagel (1991, Chap. 5). Note also that there is scope for debate about how precise these calculations need to be; see, e.g., Martins et al. (2002); this point will be addressed again below.

[5] Technically, the contrast-based approach is not the only way of interpreting the FIC. Mathematically, all the method does is calculate covariances (and variances) of an evolutionary process, which is made possible by the Brownian motion assumption. For present

While much else could be said about the workings of the method, for present purposes, the above is sufficient. What is important here is just that this method has become a staple in the investigation of (correlated) evolution—a vast array of studies rest on it to an essential degree (e.g., Ackerly and Reich 1999; Harvey and Pagel 1991, Chap. 5; Martins et al. 2002; Blomberg et al. 2003; Felsenstein 2004, Chap. 25). Despite this widespread use, however, the method is also quite controversial; the next section considers this controversy further.

Questioning the Cogency of the FIC

Ever since the FIC approach was first proposed a number of objections to it have been raised. While many of these objections have been heavily discussed (see for example the exchange in Westoby et al. 1995a, b; Harvey et al. 1995a, b), there is a recent and rather philosophical charge that has so far remained unanswered. In order to get a better sense of the dialectical place of this charge, it is best to begin by briefly sketching the other major criticisms that have been made of the FIC.

First and most famously, there is the worry that the FIC *overcorrects* for possible phylogenetic disturbing influences on the evolution of the traits in question (e.g., Westoby et al. 1995a, b; Desdevises et al. 2003). The reason for this is that the FIC takes no account whatsoever of the absolute values of the traits in question—only their differences matter. This, though, may be seen to overshoot its target considerably: *some* of the absolute values of the traits in question will represent the effects of selection (i.e., of the organism's ecology), and not of something like "phylogenetic inertia." Relatedly, it also seems that the FIC seems to focus too strongly on *change*, and ignores *stasis*—it seems that the fact that some specific trait value is being maintained in a population over time can be very meaningful as well, and ought to be taken into account as such (e.g., Westoby et al. 1995a, b; see also Sober 2008, pp. 252–253).

However, it is now widely agreed that this objection needs to be handled with care. Unless one denies that there is any kind of inheritance of traits across generations—which is clearly implausible—it somehow needs to be acknowledged that different taxa will not be statistically independent data points. It is for this reason that, by now, everybody in the literature agrees that some correction for phylogenetic influences needs to be made—what is really at stake in this debate is how, exactly, this ought to be done (see also Harvey et al. 1995a, b; Freckleton et al. 2002; Housworth et al. 2004). While complex, it seems that this is something that can be addressed by adding further considerations to the basic version of the FIC, and does not require a drastic shift away from the method (see also Freckleton et al. 2002; Lynch 1991).[6]

The second set of objections to the FIC concerns the truth of assumptions (i) and (ii)—in particular, there is the worry that these assumptions are frequently *false*. Specifically, we often do not know the exact phylogeny of the taxa in question, and even if we do know it, we often do not know the relevant branch lengths with any degree of certainty. Given the fact that that this kind of knowledge is necessary to get FIC off the ground, it might thus seem that this method is not of much practical usefulness (see also Felsenstein 1985, pp. 10–12; Harvey and Pagel 1991).

However, these sorts of worries also do not show that there is a major flaw in the FIC.[7] Primarily, this is because we often have very good *estimates* of the appropriate phylogenies and branch lengths, even though we do not really have *knowledge* of them; in turn, this will—at least in many cases—provide a sufficiently strong foundation to build the FIC on (see also Lynch 1991, pp. 1078–1079; Felsenstein 1985, 1988). This becomes particularly clear by noting that, due to the recent increases in the available amount of data (mainly because of better and cheaper gene sequencing technologies), our understanding of the tree of life—while remaining steeped in uncertainties—is, at least in part, fairly well-grounded (e.g., Ackerly and Reich 1999; Davis et al. 2007). In turn, this understanding will often be enough to make meaningful applications of the FIC possible.

The third—and for present purposes central—objection to the FIC centers on assumption (iii). To understand this objection better, it is best to begin by noting that this assumption, at least on the face of it, strongly suggests that the traits under investigation evolved purely by *drift*: if changes in X and Y are no more likely to happen in one direction rather than another, it seems that X and Y must have evolved by drift only. However, this dialectical presumption in favor of drift seems very puzzling, as it appears to sit badly with the aims of the FIC (see, e.g., Martins et al. 2002; Housworth et al. 2004). As Elliott Sober puts it:

Footnote 5 continued
purposes, though, the formulation in the text is sufficient. I thank Joe Felsenstein for useful discussion of this point.

[6] Alternatively, one might say that trying to determine the absolute values of the relevant traits or the possibility of evolutionary stasis concerning them is answering a different question from the one that motivates the FIC (and which needs different kinds of data to be answered).

[7] In fact, these worries speak to *all* kinds of comparative methods. See also Sober (2000, Chap. 6).

> If we want to test the hypothesis that selection causes lineages to evolve towards a stable optimum, the Brownian motion assumption is not appropriate. The assumptions used to test a selection hypothesis against others should be independent of which of these hypotheses is true; the assumptions should not entail that the selection hypothesis is true, but neither should they entail that it is false (Sober 2008, pp. 252–253).

It seems clear that Sober's objection here is at heart a methodological claim. His worry seems to be that the FIC begs the question against the key issues it is meant to investigate. As noted earlier, it is the aim of the FIC to provide us with evidence about the evolution of the traits under study—about whether that evolution happened by natural selection, drift, or in some other way, and about how it did so. Given that, though, it seems highly problematic that the method presumes, from the start, that the evolution of the traits it studies happened by *drift*: this seems to build a particular answer to the key question the FIC is designed to investigate right into the method itself. In short: there is something methodologically troubling about the FIC—issues that should be left open (as they are the target of the investigation) are in fact closed off by the method. In what follows, I shall call this the *methodological charge* of the FIC.

However, before discussing the methodological charge in more detail, it is useful to consider a related preliminary worry first. This worry is based on the idea that, if Sober is right that the Brownian motion assumption at the heart of the FIC is equivalent to an evolutionary model of drift, then the method seems to become *conceptually incoherent*. If it is assumed that two biological traits evolved by pure drift, then it might seem that it is not biologically plausible that they are also correlated in their evolution. Put differently: since assuming that two traits evolved by drift is assuming that they evolved *randomly*, the possibility that they evolved together would seem to be ruled out from the beginning. After all, if there is no systematic driving force like natural selection behind the evolution of these traits, there might seem to be nothing that *could* ground a meaningful correlation in their evolution. For this reason, the FIC could be regarded as conceptually flawed: it is not clear how its results are even to be understood. In what follows, I shall call this the *conceptual charge* of the FIC.

As I will make clearer momentarily, while the conceptual charge raises somewhat different questions than Sober's methodological worry, it also brings to the fore several important issues that are usefully noted in this context. Begin, therefore, by considering the conceptual charge in more detail.

The Conceptual Charge: Drift, Correlated Evolution, and Trait Modularity

The conceptual charge of the FIC rests on the idea that it is incoherent to suppose that there could be a biologically meaningful correlation in the evolution of two traits, each of which evolves by drift. Note that the restriction to biologically meaningful correlation is important, as no one doubts that there could be *spurious* correlations in any two quantities—including two traits that evolve by drift. This, though, would not seem to be something that is worth investigating for its own sake. Put differently, the conceptual charge is the claim that, given the assumption of drift underlying the FIC, every time the method finds a correlation in the evolution of two traits we should conclude that this is purely spurious, and of no genuine biological importance. However, as I try to show in what follows, this is false. In fact, there is a class of biologically important scenarios that do feature a correlation in the drift-driven evolution of two traits. This class of scenarios is constituted by cases in which two traits are causally linked in such a way that, in an individual organism, changes in one trait bring about changes in the other trait, i.e., that the two traits have a low degree of modularity with respect to each other (see also Felsenstein 1988). The following example makes this clearer.[8]

Assume that the size of an imaginary plant's leaves is adaptively neutral when it comes to all environmental factors (at least within certain limits); assume also that the same holds for the size of its fruit. More specifically, assume that, in the particular environment in question, larger leaves are no better at converting carbon dioxide into energy than smaller ones, that the plant's pollinators show no preference for larger over smaller fruits, that it is not significantly more costly to make larger fruits and leaves than smaller ones (maybe because there are abundant resources available), and so on for all other environmental factors. In turn, this suggests that the two traits' "environmental" fitness function (i.e., the function that considers all and only the environmental factors impacting the fitness of leaf and fruit size) looks as shown in Fig. 1.

Importantly, assume further that there is a direct connection between leaf size and fruit size in individual organisms, so that increases in leaf size—however they were brought about—automatically lead to increases in fruit size in these organisms. There are many reasons for the existence of such a connection. In the first place, it might be that there are genetic linkages between both traits—for example, the two traits might be pleiotropic effects of the same gene

[8] Instead of talking of modularity, some writers prefer to speak of the existence of *genetic constraints* or *additive genetic covariances* (e.g., Felsenstein 1988, 2002, 2004, Chap. 25). I favor the terminology of "modularity," as it makes clearer that the source of the connection between the traits in question need not be genetic, but can lie elsewhere as well.

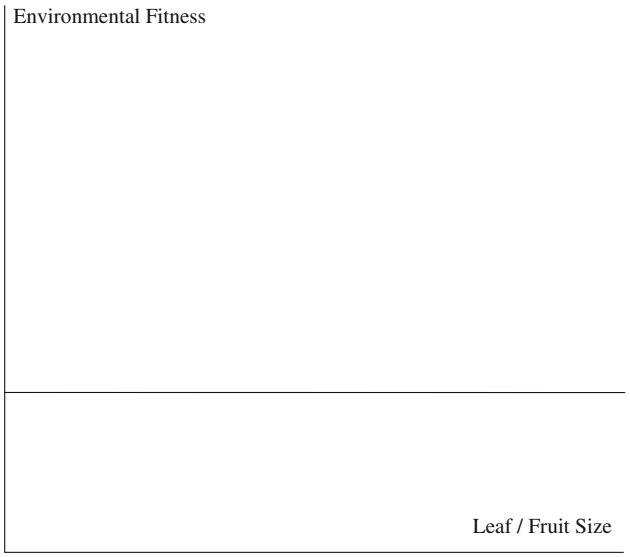

Fig. 1 Environmental fitness function for leaf and fruit size

complex (see also Felsenstein 1988). Second, it might be that the developmental programs responsible for building fruit and leaves are not entirely separate: for example, the two traits might happen to depend on similar biochemical processes going on at the appropriate times. Given this, if there is a change in these processes (for whatever reason), both traits can be expected to be affected simultaneously (see also Wagner and Altenberg 1996). Finally, there might be physical constraints on the evolution of the two traits—as in the case of body size and mass—so that the two simply could not vary independently from one another.[9]

What is important to note about cases like this is that they exemplify scenarios in which two traits are not very *modular* (or "quasi-independent") with respect to each other (Lewontin 1978; Brosnan 2009; see also Striedter 2005; Machery 2007). While the notion of trait modularity is still somewhat ill-defined, it is sufficient for present purposes to note that the modularity of a trait can, at least to a first approximation, be seen to consist in the extent to which that trait can vary independently from other traits, at least in the medium term (e.g., Simon 1962; Lewontin 1978; Carruthers 2006; Schulz 2008; Brosnan 2009; Godfrey-Smith 2009, pp. 57–59). Three points are important to note concerning this notion.

First, the *proximate cause* of the modularity of a trait concerns the extent to which the trait is linked to other traits *in an individual organism*. Second, however, "trait modularity" itself is an *ultimate* notion: traits that are highly modular can *evolve* (largely) independently from one another, whereas traits that are not cannot. Hence, the investigation of the modularity of various traits is straightforwardly part of evolutionary biology. Thirdly and finally, the modularity of a trait is a matter of degree: it is uncontroversial that no trait can vary completely independently from all the other traits of an organism, and it is also uncontroversial that it is not the case that an organism can only be a changed as a whole. What is at stake is *to what extent* any given trait can vary independently from other traits (see, e.g., Lewontin 1978; Wagner and Altenberg 1996; Schulz 2008; Brosnan 2009; Godfrey-Smith 2009).

From the perspective of the present discussion, the major point to note concerning all of this is that the FIC gives us the means for investigating the modularity of specific traits of specific types of organisms (see also Felsenstein 2002).[10] In particular, the method can help us determine exactly *how modular* various traits are in relation to each other. This is so, as for two selectively neutral traits, the greater the correlation in the independent contrasts, the less modular they are likely to be.[11] Put differently: the higher the correlation in the independent contrasts of two selectively neutral traits, the stronger the evidence that these two traits have a low degree of modularity with respect to each other. The reason for this is that a low degree of modularity is the only non-spurious candidate for the existence of evolutionary linkages between these two traits: given that the traits are assumed to have evolved by drift *and* to be evolutionarily linked, it becomes likely that they are genetically, developmentally, or physically connected—for these are the major causes for the existence of the evolutionary connection here.[12] Moreover, the degree to which they are evolutionarily correlated gives insight into the strength of the causal mechanisms connecting the two traits.

Hence, it becomes clear that, even if it is accepted (for the sake of the argument) that the FIC assumes that the traits in question evolved by drift—as the above objection claimed—a correlation in their independent contrasts, far from being conceptually suspect, turns out to be very easily understandable. Importantly, moreover, investigating the degree of modularity among various traits is theoretically and practically highly useful: for example, this kind of investigation can have important implications for the

[9] This does not appear as plausible when it comes to the present example, though.

[10] Of course, it might be claimed that investigating the degree of modularity is not normally what the FIC is *in fact* used for. However, this is not a problem for the present defense of the method: on the one hand, as made clearer below, the FIC can *also* be seen to have other aims, and on the other, the present point is merely that the FIC can be given a coherent aim *even if* it is assumed to be based on drift. See also Felsenstein (1988, 2004, Chap. 25).

[11] Note that, as such, trait modularity need not be a symmetric relation: it may be possible that one trait can vary quasi-independently of another, but not vice versa. If so, then the direction (including bi-directionality) of the modularity needs to be established separately, after a correlation in independent contrast has been found for correlations *are* symmetric (see also note 24 below).

[12] Note that this argument depends essentially on the assumption that the two traits evolved by drift. If this assumption is dropped (as is done below), the issues get more complex.

efficacy of gene therapies and—though this is somewhat controversial—the 'evolutionary potential' of the relevant organism (see e.g., Hansen et al. 2003; Wagner and Altenberg 1996).

In sum: the fact that the FIC assumes that the evolution of the traits it investigates followed a Brownian motion-like process does not mean that it is conceptually flawed. There is nothing problematic about investigating correlations in selectively neutral traits, as this can tell us something about the degree of modularity of these traits. Hence, the conceptual charge of the FIC can be successfully answered. Consider, then, Sober's methodological charge of the method.

The Methodological Charge: Brownian Motion and Selection

The methodological charge of the FIC claims that the method closes questions for discussion that should remain open. In particular, the accusation here is that, by assuming that the traits in question evolved by Brownian motion, the method presumes they have evolved by drift. This, though, should be left open (even if it is conceptually coherent), as finding out about the factors that determine the evolution of the traits is part of the motivation of using the method in the first place. Now, the most straightforward way to answer this charge is to show that the FIC *can* investigate selective hypotheses, despite being based on an assumption of Brownian motion.[13]

To show that this is in fact so, I consider three different reasons for why the Brownian motion assumption behind the FIC should not be seen to rule out the fact that the traits it investigates evolved by natural selection. First, I shall argue that Brownian motion can be used as a mathematical simplification that has no implications concerning the evolutionary processes at work. Second, I shall show that Brownian motion can be used to describe ordinary directional selection. Third, I shall show that Brownian motion can be used to describe a process that might be called "internal selection." Note that these three reasons are not mutually exclusive—they can all be true in different cases.[14] Note also that, as will become clearer below, while not completely dispelling the methodological charge of the FIC, together these three responses go quite a ways towards making it significantly less threatening.

Brownian Motion as a Harmless Idealization

The first reason for denying the cogency of the methodological charge argues that the assumption of Brownian motion at the base of the FIC should, at least at times, only be seen to function as a harmless idealization. Specifically, this assumption is often to not to be taken to describe the actual evolutionary processes that are driving the traits in question; instead, it is to be seen merely as a device for simplifying the relevant calculations—and that in a way that does not significantly bias their conclusions. In this respect, the assumption does not differ from many other idealizing assumptions used in evolutionary biology: for example, many cognitive ethological models assume unlimited memory stores, and many evolutionary game theoretic models assume infinite population sizes and completely random mating. In each of these cases, these assumptions are merely employed as helpful fictions that, while descriptively false, do not negatively bias the results of the models they are embedded in.

The same can be true in the case of the FIC and the assumption of Brownian motion (see, e.g., Diaz-Uriarte and Garland 1996; Martins et al. 2002; Housworth et al. 2004). Specifically, at least at times, there is no need to read any deeper descriptive intentions into the Brownian motion assumption of the FIC. The relevant traits are not *really* assumed to have evolved by drift—instead, the random walk assumption is employed merely to aid the relevant computations. As long as the evolutionary trajectory of these traits is not very strongly biased in one direction or another, there is no real harm in making this assumption—and it has the benefit of making the necessary calculations possible, or at least much easier (e.g., Martins et al. 2002).

It needs to be noted that there is a flip side to this argument: if there *is* strong directional selection for (one of) the traits under study, assuming they evolved by Brownian motion *will* lead the FIC to give biased results when estimating their degree of evolutionary correlation (e.g., Diaz-Uriarte and Garland 1996; Martins et al. 2002; Housworth et al. 2004).[15] Hence, this way of defending the conceptual cogency of the FIC will not always work—it is limited in its domain of applicability. However, this lack of full generality should not be seen to detract from the

[13] Note that the dialectic here is a bit complex. On the most straightforward reading of Sober's worry, he merely requires *logical* independence between the assumptions of a method and the hypotheses under study. This, though, is consistent with the assumptions and hypotheses being *probabilistically* highly non-independent (e.g., there might be exactly *one* very far-fetched scenario of selection that is consistent with the Brownian motion assumption, with all the other scenarios featuring drift only). As I try to make clearer below, though, I think that the solution defended here can apply to both readings of independence.

[14] Moreover, these three scenarios can be combined with the scenario of traits that have a low degree of modularity with respect to each other. See, e.g., Felsenstein (2002) for a model of this kind of case.

[15] In fact, the importance of these sorts of scenarios might be a key part of the motivation behind Westoby et al.'s worries concerning the FIC (e.g., Westoby et al. 1995a, b).

cogency of the defense of the FIC for a restricted class of cases. As long as it is kept in mind that the Brownian motion assumption is only sometimes cogent as an approximation of directional selection, it seems to be perfectly acceptable for it to form the basis of the FIC: the fact that the assumption is not always appropriate should not be conflated with the fact that it never is.[16]

Brownian Motion as a Model of Directional Selection

The second reason for denying the methodological charge of the FIC is based on the idea that it is generally false to assimilate the fact that the evolution of a trait follows a random walk with the fact that there is not (significant) directional selection (see also Felsenstein 1988).[17] In particular, the idea here is that the Brownian motion assumption can, at times, also be seen to model a selective process with a constantly and randomly shifting optimum.[18] This idea is familiar from population genetics: there, it has frequently been noted that, in order to make sense of the empirical data, it is often more plausible to assume there was strong selection for a constantly changing optimum, rather than weak selection for a fixed optimum (see, e.g., Gillespie 1998, p. 120). The only point that is different here is that this changing optimum is not moving uniformly in one direction, but is changing direction randomly (see also Felsenstein 1973, 1988, 2002, 2004).[19] An example might make this clearer.

Assume that a certain imaginary angiosperm species is subject to strong selection for having "deep" (saturated) coloration in its petals if there are few pollinators around, but light coloration if there are many pollinators around (this might be due to the fact that achieving a "deep" coloration is energetically costly). Further, assume that the selection pressure is strong enough that the species will be at (or near) the optimal level coloration most of the time. Finally, assume that the number of pollinators changes randomly over time (e.g., due to the fact that this number is sensitive to various randomly fluctuating ecological factors—like ambient temperature during the hatching season). Given all of this, the evolution of petal coloration in the angiosperm species in question might end up following a random walk. Importantly, though, this is despite—and in fact because of—there being strong directional selection for petal coloration.

In short: the second reason for doubting the cogency of the methodological charge of the FIC has it that what looks like evolution due to pure drift might in fact be evolution by (strong!) natural selection for a randomly changing optimal value. Of course, just as before, this defense of the methodological cogency of the FIC will not always be equally plausible: not all cases of natural selection feature randomly changing optima. However, and also just as before, this limitation of the defense should not be overstated.

First, cases of randomly changing optima seem sufficiently common to make the present defense of the FIC interesting: as suggested by the above example, such cases can come about for a variety of reasons, and should be seen to be plausible hypotheses in many evolutionary investigations. Second, the present response can be used in conjunction with the previous one to make a strong case for the methodological acceptability of the Brownian motion assumption: if the goal is to capture weak unidirectional selection, then the Brownian motion might be useful as a harmless idealization[20]; if the goal is to capture strong selection with a randomly changing optimum, then the Brownian motion assumption might be useful as an accurate description of reality. Third, just as before, it needs to be kept in mind that just because a method is limited in its applicability, this does not mean that it is methodologically flawed: it is one thing not to be able to investigate all cases of natural selection, but quite another not to be able to investigate any (I will return to this point below). Consider, then, the final reason for doubting the methodological charge of the FIC.

Brownian Motion as a Model of Internal Selection

This third reason is based on the idea that, even if the assumption of Brownian motion is seen to rule out that traits *X* and *Y* are adaptations to some environmental factor, it is still consistent with them being adaptations to *each other*. In other words, the claim here is that the FIC can often be seen to investigate selective hypotheses according to which the source of the selection lies in the organism's *internal constitution*, not in its *external environment*.[21] In

[16] In fact, the same is true for all idealizations.

[17] I thank David Baum for some useful remarks about this point.

[18] It is also interesting to note that precisely this is sometimes assumed in methods based on phylogenetic least squares (see also note 1).

[19] It seems that Sober (2008) wants to exclude this scenario from consideration by his insistence that we investigate "stable optima" only. However, it is not clear why he would do this, given the importance of moving optima.

[20] We might also consider the possibility of "internal selection" in this context—see below for more on this.

[21] Note that "internal" here merely means that the trait in question is an adaptation to features that are somehow *part of* the organism. It does not mean that these features must be on the "inside" of the organism (whatever exactly this may be taken to mean); in fact, in the example to follow, both leaves and fruit are *not* internal in this latter sense.

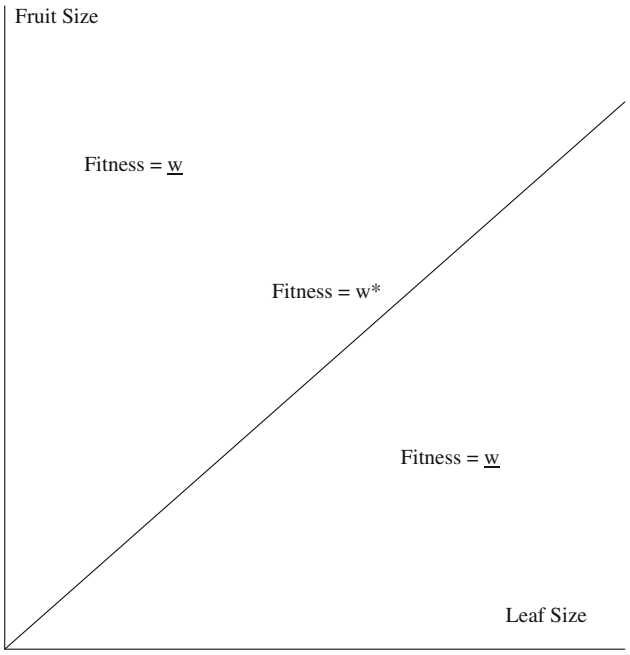

Fig. 2 The iso-fitness curve for different fruit and leaf sizes

order to make this idea clearer, let us return to the example of the fruit and leaves mentioned earlier.

Just like before, assume that fruit and leaf sizes are selectively neutral when it comes to all environmental factors (so that the environmental fitness function of the two traits is still as in Fig. 1). However, assume further that certain *combinations* of fruit and leaf sizes are selectively advantageous, in the sense that it will be adaptive for the plant to have larger fruits *given that* it has larger leaves (though it is not, as such, adaptive for it to either have large leaves or larger fruits). One reason for this kind of "interaction effect" between fruit and leaf sizes may be that the plant's fruits are more easily noticed by its pollinators if they stand in a certain fixed ratio to its leaves, viz., if they are neither too big nor too small (again keeping in mind, though, that the size of the fruit *by itself* has no impact on its being noticed by potential pollinators). For this reason, if there is a random increase in leaf size, this will make it adaptive for the plant to increase its fruit size as well—and vice versa.[22]

Hence, fruit size here can be seen as an adaptation—just not as an adaptation to an external factor, but as one to another part of the plant: it is a selective response to increases in leaf size (and not to changes in pollination patterns in and of themselves). Graphically, this therefore suggests that the organism's iso-fitness curve, i.e., those combinations of leaf and fruit size that leave the organism's (overall) fitness unchanged, is as shown in Fig. 2.[23]

In the present context, what is most important about this example is that it again makes clear that the FIC *can* investigate interesting selective hypotheses, despite being based on an assumption of Brownian motion. In particular, the example shows that this assumption does not prevent the FIC from investigating the situation where two or more traits have the biological function to deal with each other: in fact, the establishment of a correlation in independent contrasts between these traits is some of the best evidence for this kind of scenario available.[24]

Hence, there is again reason to doubt the cogency of the methodological charge of the FIC: the method is perfectly capable of investigating important selective scenarios. Of course, just as above, it is important to note the caveat that this use of the FIC is limited to certain kinds of selective hypotheses—not every case of selection is of the "internal" variety. However, just as above, this should not be seen as a major flaw of the method as such: virtually every theoretical tool in biology (and in science in general) is limited in applicability.

Tacking stock, what all of this means is that, contrary to Sober's objection, there are numerous cases of selection that can be cogently investigated by the FIC. Specifically, the assumption of Brownian motion can be used to approximate many cases of weak to moderate unidirectional "external" selection, it can describe all cases of random-directional external selection, and it can describe all cases of internal selection. Hence, there is no reason to conclude that the method is *completely* methodologically flawed due to its being based on an assumption of Brownian motion.

However, it also needs to be acknowledged that there are some selective scenarios—strong unidirectional external selection for example—that are out of reach of the method. For this reason, the present defense can only *mitigate* Sober's worry—it cannot fully resolve it. In this

[22] Another good example for this sort of scenario might be camouflaging coloration in various animals. In order for such a coloration to be successful in hiding the animal, it might matter that the patterns it involves stand in the right relationships to each other; however, it might otherwise be irrelevant what size the individual patterns are.

[23] Figure 2 assumes that all combinations of leaf and fruit size that are non-optimal have the same level of fitness; however, this can be changed at the cost of further complications (essentially, one can make the fitness landscape three-dimensional, and let fitness drop off non-uniformly and continuously as one moves away from the line in Fig. 2).

[24] It does need to be noted, though, that the FIC cannot establish which of the two traits is the adaptation and which is the "internal environment," or if both traits are adaptations to each other. In order to establish *this*, another method is needed—for example, increases in one trait must be brought about artificially in the lab, and the fitness of organisms that differ in the second trait must be measured. However, this issue can be tackled separately from the one at stake here, and does not invalidate the present conclusion in any way. See also above in note 11.

regard, the methodological charge is a more worrisome objection to the FIC than the conceptual charge (which can be fully resolved). Still, though, it must also be noted that the force behind the present response is quite considerable: between them, the three selective scenarios laid out above comprise a significant part of the landscape of selective hypotheses that we might want to investigate.[25] These scenarios allow us to consider different forms of traditional external selection, and they allow us to consider the slightly less common, but no less interesting, case of internal selection. Hence, the possibility to investigate the above three selective scenarios should be seen to be sufficient to vindicate at least the *overall* plausibility—and certainly the widespread acceptance of the FIC.

Individuals, Populations, and Independent Contrasts

Before concluding, it is useful to briefly make more explicit the contrast between the arguments presented in the context of the defense of the conceptual charge of the FIC—where the method was shown to be concerned with investigating the *modularity* of two traits—and those presented in the context of the defense of methodological charge of the FIC—where the method was shown, among others, to be concerned with investigating two (or more) traits that are internal adaptations to each other. The usefulness of doing this derives from the fact that, at least on the face of it, these two scenarios seem very similar to each other: both feature traits with a flat environmental fitness function, and both see changes in one of these traits as engendering changes in the other trait. This might make it puzzling as to why one of these scenarios was discussed under the heading of drift, and the other under the heading of (internal) selection. However, beneath these superficial similarities, there are some major differences between these two scenarios that it is useful to point out here.

These differences primarily concern the location of the source of the connection between the traits in question: in the modularity-based case, this source is located on the *individual level*—there, changes in one trait cause changes in the other in a particular individual (e.g., because of the presence of various biochemical or physical connections between the traits). In the case of internal selection, the source is located on the *population level*—there, those organisms in the population whose expressions of the traits (for whatever reason) are in the appropriate ratio to each other do better than those for which this expression is in the wrong ratio (see also Sober 1984). Put differently, in cases of internal selection, no deep physical or biochemical connections between the traits in individual organisms need to be presumed to exist; by contrast, in cases of low trait modularity, the existence of these connections is precisely what is at issue.

This is an important point to note, as it goes beyond the issues surrounding the FIC at stake here. In particular, the present discussion shows that, in general, correlated evolution can come about through very different causal routes operating at very different levels: it could be due to proximate connections in the traits in individual organisms, or it could be due to adaptive links between these traits in a population of organisms.[26] Keeping this distinction in mind is necessary to get a proper understanding of correlated evolution, and has many further important implications—for example, when it comes to various natural or experimental interventions, or in respect to the study of the mechanisms that bring about causal connections between various traits in individuals organisms.[27] Hence, the present discussion holds lessons beyond those concerning the FIC—it illustrates issues that arise in the study of correlated evolution quite generally.

Conclusion

I have argued that it is possible to at least mitigate Sober's recent objection to the FIC. Specifically, I have tried to show, first, that a related conceptual objection to the method—the claim that it is conceptually incoherent to suppose that there could be two selectively neutral traits that are evolutionarily correlated—does not pose a major threat to the cogency of the FIC. In this case, the target of the method should simply be seen as the investigation of the modularity of the relevant traits. Second, when it comes to Sober's methodological objection more specifically, viz., the claim that the method closes off the possibility that the relevant traits have evolved by natural selection, its force should not be overstated either. In this case, it can be

[25] This is also important in the context of the point raised in note 13 above.

[26] In fact, both of these could be true at the same time: for example, it might be adaptive for two traits to stand in a certain ratio with respect to each other, but certain instances of this ratio might also be physiologically determined (e.g., if fruit become sufficiently large, larger leaves might be a physical necessity; at any point, though, only a certain ratio of fruit and leaf size is adaptive).

[27] Note that what the FIC, specifically, can add to this study is to provide (a) a quick check to see whether there are any linkages among the relevant traits that it would be useful to investigate further, and (b) partial evidence of the degree of modularity and evolutionary history of the relevant traits (using further experimental data to supply the relevant missing premises—see also notes 12 and 24). Neither of these contributions should be underrated. Finally, note that this issue is neutral concerning the debate whether natural selection can also have effects in individual organisms; for more on this debate, see, e.g., Neander 1995; Sober 1995; Bouchard and Rosenberg 2004; Forber 2005; Millstein 2006.

shown that, in fact, the FIC *can* investigate various selective hypotheses (either because the assumption of Brownian motion it rests on is merely used as an idealizing mathematical tool, or because it is in fact consistent with certain selective scenarios). While this cannot fully resolve Sober's objection, it can at least go a significant part of the way towards doing so.

Overall, I have thus tried to show that on the one hand, there are no conceptual or methodological concerns that speak against the FIC deservedly holding a central place in the (evolutionary) biologist's toolkit. On the other, I have tried to show that correlated evolution can come about both due to causes that work on the population level and those that work on the individual level. For these reasons, the issues discussed here hold an interest for anyone concerned with deepening our understanding of the way biological evolution works.

Acknowledgments I would like to thank Elliott Sober, David Baum, Joseph Felsenstein, and audiences at the University of Bristol, Exeter University, and the London School of Economics and Political Science for useful remarks on previous versions of this article.

References

Ackerly DD, Reich PB (1999) Convergence and correlations among leaf size and function in seed plants: a comparative test using independent contrasts. Am J Bot 86:1272–1281

Blomberg SP, Garland T Jr, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745

Bouchard F, Rosenberg A (2004) Fitness, probability, and the principles of natural selection. Br J Philos Sci 55:693–712

Brosnan K (2009) Quasi-independence, fitness, and advantageousness. Stud Hist Philos Biol Biomed Sci 40:228–234

Bulmer M (1991) Use of the method of generalized least squares in reconstructing phylogenies from sequence data. Mol Biol Evol 8:868–883

Carruthers P (2006) The architecture of the mind. Oxford University Press, Oxford

Davis CC, Latvis M, Nickrent DL, Wurdack KJ, Baum DA (2007) Floral gigantism in Rafflesiaceae. Science 315:1812

Desdevises Y, Legendre P, Azouzi L, Morand S (2003) Quantifying phylogenetically structured environmental variation. Evolution 57:2647–2652

Diaz-Uriarte R, Garland T Jr (1996) Testing hypotheses of correlated evolution using phylogenetically independent contrasts: sensitivity to deviations from Brownian motion. Syst Biol 45:27–47

Felsenstein J (1973) Maximum likelihood estimation of evolutionary trees from continuous characters. Am J Hum Genet 25:471–492

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1–15

Felsenstein J (1988) Phylogenies and quantitative characters. Annu Rev Ecol Syst 19:445–471

Felsenstein J (2002) Quantitative characters, phylogenies, and morphometrics. In: MacLeod N (ed) Morphology, shape, and phylogenetics. Systematics Association Special, vol 64. Taylor and Francis, London, pp 27–44

Felsenstein J (2004) Inferring phylogenies. Sinauer, Sunderland

Forber P (2005) On the explanatory roles of natural selection. Biol Philos 20:329–342

Freckleton RP, Harvey PH, Pagel M (2002) Phylogenetic analysis and comparative data: a test and review of evidence. Am Nat 160:712–726

Gillespie J (1998) Population genetics: a concise guide. John Hopkins University Press, Baltimore

Godfrey-Smith P (2009) Darwinian populations. Oxford University Press, Oxford

Hansen TF, Pélabon C, Armbruster WS, Carlson ML (2003) Evolvability and genetic constraint in Dalechampia blossoms: components of variance and measures of evolvability. J Evol Biol 16:754–766

Harvey P, Pagel M (1991) The comparative method in evolutionary biology. Oxford University Press, Oxford

Harvey P, Read A, Nee S (1995a) Why ecologists need to be phylogenetically challenged. J Ecol 83:535–536

Harvey P, Read A, Nee S (1995b) Further remarks on the role of phylogeny in comparative ecology. J Ecol 83:733–734

Housworth EA, Martins EP, Lynch M (2004) The phylogenetic mixed model. Am Nat 163:84–96

Lewontin RC (1978) Adaptation. Sci Am 239(3):156–169

Lynch M (1991) Methods for the analysis of comparative data in evolutionary biology. Evolution 45:1065–1080

Machery E (2007) Massive modularity and brain evolution. Philos Sci 74:825–838

Martins EP, Diniz-Filho JAF, Housworth EA (2002) Adaptive constraints and the phylogenetic comparative method: a computer simulation test. Evolution 56:1–13

Millstein R (2006) Natural selection as a population-level causal process. Br J Philos Sci 57:627–653

Neander K (1995) Pruning the tree of life. Br J Philos Sci 46:59–80

Schulz A (2008) Structural flaws: massive modularity and the argument from design. Br J Philos Sci 59:733–743

Simon HA (1962) The architecture of complexity. Proc Am Philos Assoc 106:467–482

Sober E (1984) The nature of selection. University of Chicago Press, Chicago

Sober E (1995) Natural selection and distributive explanation: a reply to Neander. Br J Philos Sci 46:384–397

Sober E (2000) Philosophy of biology, 2nd edn. Westview, Boulder

Sober E (2008) Evidence and evolution. Cambridge University Press, Cambridge

Striedter G (2005) Principles of brain evolution. Sinauer, Sunderland

Wagner GP, Altenberg L (1996) Complex adaptations and the evolution of evolvability. Evolution 50:967–976

Westoby M, Leishman MR, Lord JM (1995a) On misinterpreting the "phylogenetic correction". J Ecol 83:531–534

Westoby M, Leishman MR, Lord JM (1995b) Further remarks on phylogenetic correction. J Ecol 83:727–729